

REVISION OF THE *AMEIVA* (REPTILIA: TEIIDAE) OF THE
ANGUILLA BANK, WEST INDIES

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ABSTRACT

The ground lizards (*Ameiva*) of the Anguilla Bank and Sombrero, Lesser Antilles, are revised. The nomenclatural history is reviewed and clarified. *Ameiva corvina* is reviewed in relation to *A. plei*. Two subspecies of *Ameiva plei* (*A. p. plei* and *A. p. analifera*) are recognized and one new species (*A. corax*) is named on the basis of a combination of meristic and pattern characteristics. Temporal variation in the Sombrero population and melanistic races of *Ameiva* are discussed. This is the first report of two species of *Ameiva* occupying one island bank in the Lesser Antilles.

INTRODUCTION

The Lesser Antilles extend northward from South America in a long arc of more than a dozen major islands and hundreds of minor islets. These islands are clustered on undersea banks, each of which was emergent as one large island until the post-Pleistocene rise in sea levels. As sea levels rose each large island fragmented into many smaller ones. The northernmost of the major islands—Anguilla, St. Martin (including St. Maarten) and St. Barthélemy—lie on the Anguilla Bank (Christman, 1953). Thirty-two miles northwest of the Anguilla Bank lies Sombrero, a small, isolated island east of Puerto Rico and the Virgin Islands.

Baskin and Williams (1966) reviewed the *Ameiva* of the Lesser Antilles and recognized 11 species, each endemic to either an island or a bank. Among the species they recognized were *Ameiva plei* on the Anguilla Bank and *Ameiva corvina* from Sombrero. Here we review variation and systematics of the *Ameiva plei* group, which is composed of the *Ameiva* on the Anguilla Bank. We also review the systematics of *Ameiva* from Sombrero. One new species is described and two subspecies of *A. plei* are recognized. Melanistic populations are compared and discussed in relation to ecological and physiological factors. An electrophoretic analysis of these populations is being conducted, and a long-term behavioral and ecological study is in progress on the Anguilla and Dog Island populations.

MATERIALS AND METHODS

A combination of meristic and pattern characters was used to analyze geographic variation in populations of *Ameiva plei* and *A. corvina*. Five standard scale counts were taken: (1) number of dorsal granules in a line around midbody (GAB); (2) total number of femoral pores (both legs); (3) number of scales in the fifteenth caudal verticil; (4) number of subdigital lamellae on the fourth toe of the right hind foot; (5) number of transverse rows of enlarged ventral scales. These counts are consistent with those taken in other studies of teiid lizards and are therefore useful for comparison. Color and pattern were also recorded. Size is expressed as snout-vent length (SVL). Summaries of these counts including mean, range of variation, standard error, and sample size are given for each island population in Table

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Table 1.—Summaries of data for all island populations studied (includes mean, standard error, range of variation, and sample size).

	Midbody granules	Ventral scales
St. Barthélemy	160.3 ± 1.16 (142–176) N = 30	32.0 ± 0.17 (30–34) N = 34
Fregate	162.9 ± 2.47 (149–176) N = 10	32.3 ± 0.26 (31–34) N = 10
Ile Fourche	153.8 ± 1.76 (142–168) N = 18	33.1 ± 0.24 (32–36) N = 17
St. Martin/Maarten	160.3 ± 0.93 (145–178) N = 51	32.5 ± 0.11 (31–35) N = 55
Anguilla	163.3 ± 0.88 (146–185) N = 88	31.5 ± 0.12 (29–34) N = 92
Scrub	161.8 ± 1.64 (143–179) N = 22	32.3 ± 0.22 (30–34) N = 22
Little Scrub	144.0 ± 1.01 (127–159) N = 51	33.2 ± 0.21 (30–37) N = 53
Prickly Pear	154.4 ± 1.79 (149–160) N = 7	32.4 ± 0.26 (31–33) N = 8
Dog	145.0 ± 1.84 (135–159) N = 15	32.1 ± 0.23 (30–34) N = 18
Sombrero	147.7 ± 2.40 (139–156) N = 16	34.1 ± 0.31 (32–37) N = 16

1, and for each taxon in Table 2. Comparisons between taxa for each character are given in Table 3. A total of 569 specimens was examined.

Discriminant function analysis (SPSS/PC software) was performed using each island population as an operational taxonomic unit (OTU). This "natural" division for classification resulted in only 56% of the cases being correctly classified. It was apparent that islands did not define taxon boundaries. We therefore used an independent t-test (ABSTAT software) to determine the significance (0.05 level) of differences between populations for each character (Table 3). On the basis of the t-test, populations were combined into four OTUs [Sombrero, Little Scrub, St. Martin, and Anguilla-St. Barthélemy—all satellites (=Anguilla/St. Barts)]. Discriminant function analysis was then performed on these OTUs using all variables except sex and SVL.

The following collections were utilized: Academy of Natural Sciences, Philadelphia (ANSP); Natural History Museum, London (BMNH); Carnegie Museum of Natural History (CM); Museum of Natural History, University of Kansas (KU); Los Angeles County Museum of Natural History (LACM); Museum of Comparative Zoology, Harvard University (MCZ); Muséum National d'Histoire Naturelle, Paris (MNHN); Rijksmuseum van Natuurlijke Historie, Leiden (RMNH); Florida State Museum (UF); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); National Museum of Natural History (USNM).

NOMENCLATURAL HISTORY

Duméril and Bibron (1839) described *Ameiva plei* and cited the type locality as "Martinique and St. Domingue". However, *A. plei* does not occur on either island. The specimen from "St. Domingue" is not *A. plei* and is discussed later. No *Ameiva* now occur on Martinique, although *A. major* may have occurred there (Baskin and Williams, 1966). There has been much confusion about Plée's collecting localities (Stejneger, 1904:557, 622; Barbour, 1915:73). Plée apparently collected on various French islands, probably during a trip from Puerto Rico to Martinique. The specimens were shipped from Martinique to the Paris Museum in 1826, after Plée's death (Brygoo, 1989). At the museum they were recorded as being from Martinique. The type specimens of *A. plei* probably came from St. Barthélemy, a French island on the Anguilla Bank which is located along Plée's route between Puerto Rico and Martinique. Although the French claimed St. Barthélemy in the early 1700s, they sold it to Sweden in 1784 and did not reclaim it until 1877. The type specimens of *A. plei* were collected during or before 1839, when Sweden owned the island. However, as Sweden was not at war with France, Plée presumably would have been allowed access to the island. Therefore, we retain the emended type locality of Barbour and Noble (1915): "probably St. Barthélemy". Barbour and Noble (1915) mistakenly suggested that MCZ 4357 is one of the syntypes of *A. plei* and Cochran (1941), also incorrectly, stated that two of the three syntypes are from Puerto Rico.

Table 1.—Continued.

4th toe lamellae	15th caudal verticil	Femoral pores
34.2 ± 0.30 (29–37) N = 32	30.9 ± 0.30 (28–34) N = 34	45.0 ± 0.46 (40–53) N = 34
33.3 ± 0.53 (30–35) N = 12	32.0 ± 0.42 (30–35) N = 12	43.0 ± 0.52 (41–47) N = 12
33.8 ± 0.34 (31–36) N = 18	30.8 ± 0.35 (29–34) N = 18	45.3 ± 0.54 (41–48) N = 18
36.6 ± 0.25 (32–41) N = 49	32.3 ± 0.22 (28–38) N = 53	45.9 ± 0.39 (41–56) N = 52
34.4 ± 0.19 (30–38) N = 95	30.9 ± 0.16 (27–36) N = 96	45.4 ± 0.27 (37–51) N = 94
33.2 ± 0.50 (29–38) N = 23	30.4 ± 0.29 (28–33) N = 20	46.5 ± 0.57 (41–52) N = 22
36.8 ± 0.30 (33–42) N = 58	33.2 ± 0.25 (28–38) N = 57	62.1 ± 0.40 (58–72) N = 58
36.8 ± 0.37 (35–38) N = 8	28.8 ± 0.31 (28–30) N = 8	46.3 ± 1.36 (42–53) N = 7
33.7 ± 0.49 (30–37) N = 18	29.9 ± 0.32 (28–33) N = 18	45.9 ± 0.44 (42–49) N = 17
38.1 ± 0.54 (34–41) N = 15	33.3 ± 0.58 (29–38) N = 17	57.3 ± 0.80 (50–63) N = 16

The nomenclatural history of *Ameiva plei* is also confused. Three names have been proposed for Anguilla Bank *Ameiva: plei* Duméril and Bibron (1839), from “probably St. Barthélemy;” *analifera* Cope (1869), from St. Martin and St. Barthélemy; and *garmani* Barbour (1914), from Anguilla. In addition, Boulenger (1885) synonymized *A. scutata* Gray with *A. plei*, although the original description of *A. scutata* was vague and no locality data were given. Baskin and Williams (1966) synonymized *A. nevisana* (Schmidt, 1920) with *A. plei* after examining the type specimen, instead of following Barbour’s (1930) suggestion that *A. nevisana* be synonymized with *A. griseoldi*. Baskin and Williams (1966) also concluded that the type locality of *A. nevisana*, originally given as “Nevis Island, British West Indies,” was incorrect. In addition, numerous authors (Barbour, 1930, 1937; Grant, 1932) have erroneously listed *Ameiva exsul* from Anguilla.

We have retained the original spelling of the name *plei*. The International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1985:Article 31a, ii) specifies that when forming a name from a personal name (male), an “i” is added to the stem of the name. The stem of the name is determined by action of the original author.

RESULTS

The four OTUs were compared using discriminant function analysis. Function 1 (Eigenvalue 7.0309) separated the OTUs on the basis of number of femoral pores and, to a lesser extent, number of granules around the body. The only variable of Function 2 (Eigenvalue 0.3778) that is significant is the number of subdigital lamellae (Table 4). Analysis of OTU centroids reveals that the means of Function 1 for the Anguilla/St. Barts OTU and the St. Martin OTU (–1.646 and –1.090 respectively) are similar. The means for the Little Scrub OTU and the Sombrero OTU are more similar to each other than to either of the other OTUs (4.982 and 4.154 respectively) (Fig. 1). Using this designation of OTUs results in 82% of the lizards being correctly classified (Table 5). Misclassification occurs only between similar OTUs (i.e., Sombrero and Little Scrub or St. Martin and Anguilla/St. Barts).

The combination of meristic data and geological history of the islands leads us to the following conclusions: 1) there are two subspecies of *A. plei* (*A. plei plei* on Anguilla, St. Barts, and all satellite islands including Tintamarre; and *A. plei analifera* on St. Martin); 2) *A. corvina* on Sombrero is a separate species; 3) the population from Little Scrub Island is a third species, *A. corax*, n. sp. (Fig. 2).

Table 2.—Summaries of data for each subspecies (same data as in Table 1).

	Midbody granules	Ventral scales	4th toe lamellae
<i>plei plei</i>	159.8 ± 0.68 (135–179) N = 181	31.9 ± 0.09 (29–36) N = 194	34.2 ± 0.14 (29–38) N = 197
<i>plei analifera</i>	160.3 ± 0.93 (145–178) N = 51	32.5 ± 0.11 (31–35) N = 55	36.6 ± 0.25 (32–41) N = 49
<i>corax</i>	144.0 ± 1.01 (127–159) N = 51	33.2 ± 0.21 (30–37) N = 53	36.8 ± 0.30 (33–42) N = 58
<i>cornina</i>	147.7 ± 2.40 (139–156) N = 16	34.1 ± 0.31 (32–37) N = 16	38.1 ± 0.54 (34–41) N = 15
	15th caudal verticil	Femoral pores	
<i>plei plei</i>	30.6 ± 0.11 (27–36) N = 197	45.5 ± 0.18 (37–53) N = 195	
<i>plei analifera</i>	32.3 ± 0.22 (28–38) N = 52	45.9 ± 0.39 (41–56) N = 52	
<i>corax</i>	33.2 ± 0.25 (28–38) N = 57	62.1 ± 0.40 (58–72) N = 58	
<i>cornina</i>	33.3 ± 0.58 (29–38) N = 17	57.3 ± 0.80 (50–63) N = 16	

Table 3.—Scutellation data for four subspecies are compared. Plus sign denotes a statistically significant difference; minus sign indicates no significant difference; (includes sample size, mean, two standard errors).

			<i>plei</i>	<i>analifera</i>	<i>corax</i>	<i>corvina</i>
Granules						
<i>plei</i>	181	159.8 ± 1.36	X	—	+	+
<i>analifera</i>	51	160.3 ± 1.86		X	+	+
<i>corax</i>	51	144.0 ± 2.02			X	—
<i>corvina</i>	25	139.8 ± 3.16				X
Fourth toe lamellae						
<i>plei</i>	197	34.2 ± 0.28	X	+	+	+
<i>analifera</i>	49	36.6 ± 0.50		X	—	+
<i>corax</i>	58	36.8 ± 0.60			X	+
<i>corvina</i>	24	40.5 ± 1.10				X
Ventral scales						
<i>plei</i>	194	31.9 ± 0.18	X	+	+	+
<i>analifera</i>	55	32.5 ± 0.22		X	+	+
<i>corax</i>	53	33.2 ± 0.42			X	+
<i>corvina</i>	25	35.4 ± 0.60				X
Fifteenth caudal verticil						
<i>plei</i>	197	30.6 ± 0.22	X	+	+	+
<i>analifera</i>	52	32.3 ± 0.44		X	+	+
<i>corax</i>	57	33.2 ± 0.50			X	—
<i>corvina</i>	25	33.0 ± 0.78				X
Femoral pores						
<i>plei</i>	195	45.5 ± 0.36	X	—	+	+
<i>analifera</i>	52	45.9 ± 0.78		X	+	+
<i>corax</i>	58	62.1 ± 0.80			X	+
<i>corvina</i>	24	62.4 ± 2.72				X

SYSTEMATIC ACCOUNT

Ameiva plei plei Duméril and Bibron, new combination

Ameiva plei Duméril and Bibron, 1839:114.

Ameiva scutata Gray, 1845:19.

Ameiva analifera Cope, 1869:158 (part).

Ameiva pleii: Boulenger, 1885:354 (emendation).

Ameiva garmani Barbour, 1914:312.

Ameiva nevisana Schmidt, 1920:1.

Ameiva pleeii: Underwood, 1962:88 (emendation).

Ameiva pleei: Baskin and Williams, 1966:154 (emendation).

Lectotype.—MNHN 4163 (here designated), an adult female from “Martinique” (probably St. Barthélemy), collected by Plée.

Paralectotypes.—MNHN 2648, same data as lectotype; MNHN 1784, an intermediate-sized specimen of *Ameiva chrysolaeama* (Duméril and Bibron, 1839), said to be from “St. Domingue”.

Diagnosis.—A subspecies of *Ameiva plei* characterized by a combination of high number of dorsal granules at midbody, low femoral pore count, low number of subdigital lamellae on the fourth toe, low number of scales in the fifteenth caudal verticil and low number of transverse rows of enlarged ventral scales (Table 2). This subspecies is large (males to 181 mm, females to 139 mm SVL), although maximum size varies (see interisland variation). Adults are gray-brown (some-

Table 4.—Pooled-within-group correlation between discriminating variables and canonical variables.
* Significant at 0.05 level.

	Function 1	Function 2	Function 3
Femoral pore	0.86623*	-0.17927	-0.12874
Granules	-0.34431*	-0.05092	0.10699
Subdiglamel	0.30367	0.78542*	0.15081
Caudalrow	0.23222	0.21667	0.68853*
Bellyplate	0.28180	0.51912	-0.58412*

times with a greenish-blue tinge) with white spots along the flanks, extending onto the back posteriorly, sometimes coalescing to form vertical white bars. Young specimens are brown with seven light stripes (some broken). Ventral scales are bluish-white to white and patternless, and populations on some islands have two dark longitudinal stripes on the ventral side of the tail.

Distribution.—Anguilla, Scrub Island, Upper (eastern) Prickly Pear Cay, Dog Island, Scilly Cay, Ile Tintamarre, St. Barthélemy, Ile Fourche, Ile Frégate, Ile Toc Vers, Ile Chevreau (Figure 2).

Description of lectotype.—An adult female measuring 126 mm SVL, tail broken. The color and pattern were described by Duméril and Bibron (1839). Femoral pores 23 and 21 (total 44); 31 scales in the fifteenth caudal vertical; fourth toe subdigital lamellae 32 (right foot); 32 transverse rows of enlarged ventral scales.

Variation.—*Ameiva plei plei* is a highly variable striped or spotted subspecies. Interisland variation is described below. In general, the smallest specimens (40 mm–74 mm SVL) are distinctly striped, with a light brown dorsal stripe (sometimes interrupted by the dark brown ground color) and cream-colored paravertebral stripes extending from the occipitals to the groin and sometimes onto the tail. White dorsolateral stripes extend from above the eye onto the tail, and lateral stripes run from the ear to the hind leg and onto the foot. The legs have light-colored spots. The background color is dark brown with very faint light spots. Specimens ranging in size from 64 mm to 84 mm SVL have faded stripes; the vertebral stripe is the least distinct.

Specimens between 80 mm about 100 mm SVL have faint striping anteriorly with spots on the flanks and posterior dorsum. The background color is brown or gray. This pattern is most common in lizards between 80 and 93 mm, but may persist to the size of 134 mm SVL. In some smaller specimens (83 mm–92 mm SVL), but generally in specimens over 100 mm SVL, stripes are absent and the pattern consists entirely of white to greenish-white spots along the flanks and

Table 5.—Classification results.

Actual group	No. of cases	Predicted group membership			
		1	2	3	4
1	160	128	0	0	32
		80.0%	0.0%	0.0%	20.0%
2	26	0	21	5	0
		0.0%	76.9%	19.2%	3.8%
3	43	0	7	36	0
		0.0%	16.3%	83.7%	0.0%
4	41	5	0	0	36
		12.2%	0.0%	0.0%	87.8%

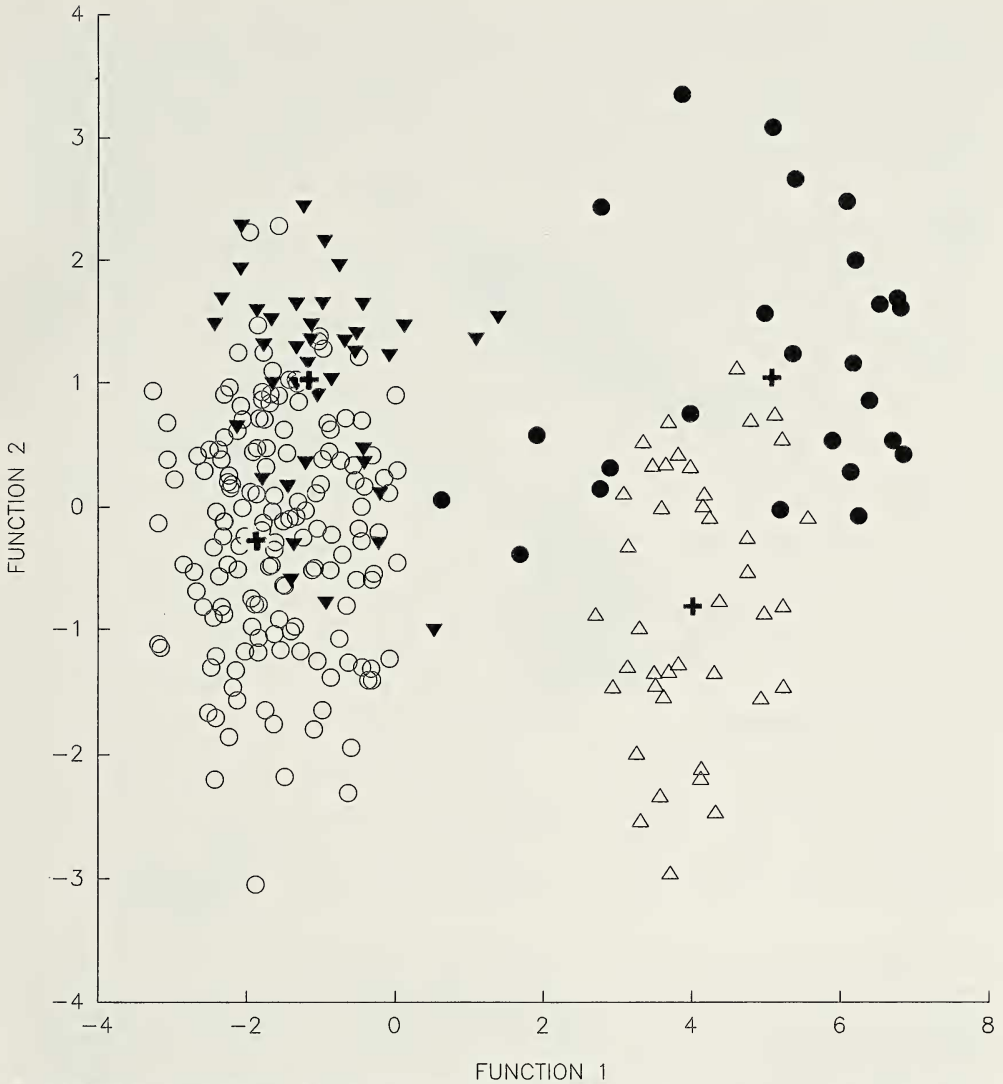


Fig. 1.—Plot of discriminant scores for Function 1 and Function 2. Open circle, *plei plei*; closed triangle, *plei analifera*; closed circle, *corax*; open triangle, *corvina*; plus signs, centroids.

posteriorly on the back. The spots are usually arranged in transverse rows and may connect to form bars. The tail and legs are spotted. The background color is gray or gray-brown, with a greenish-blue tinge in some specimens. The belly is white in all size classes. There may be some suffusion of black in the dorsal area between the forelegs, but the black pigment never forms bars. Some specimens have two black subcaudal stripes. Scale count variation is given in Table 2.

Interisland variation.—Specimens from St. Barthélemy are greenish-brown with blue-green sides. They are heavily spotted, with pale green to cream-colored spots covering the posterior two-thirds of the dorsum. These spots are usually distinct and rarely join to form bars. In specimens with stripes the pattern is distinct, however the vertebral and paravertebral stripes may be very faint and broken into spots posteriorly.

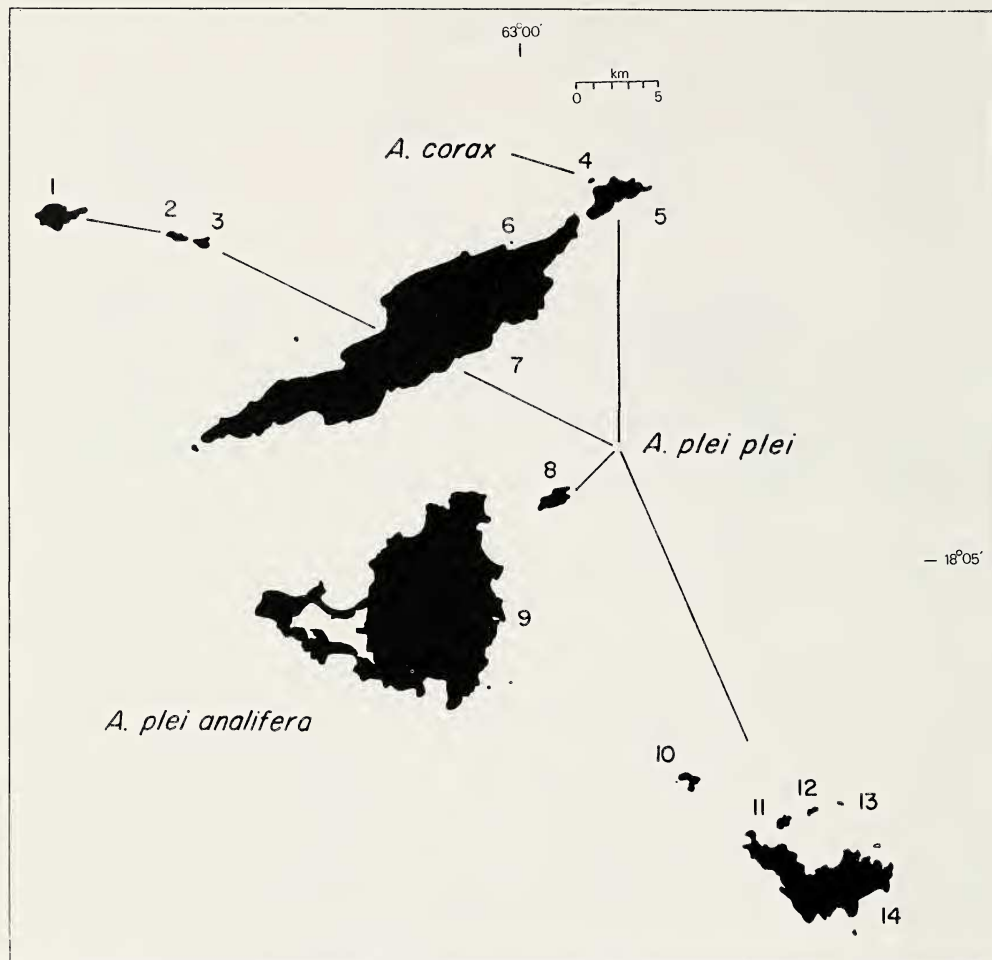


Fig. 2.—Islands of the Anguilla Bank showing distributions. 1) Dog Island, 2) Lower Prickly Pear Cay (no lizards), 3) Upper Prickly Pear Cay, 4) Little Scrub Island, 5) Scrub Island, 6) Scilly Cay, 7) Anguilla, 8) Tintamarre, 9) St. Martin/St. Maarten, 10) Ile Fourche, 11) Ile Chevreau, 12) Ile Frégate, 13) Ile Toc Vers, 14) St. Barthélemy. Sombrero Island (*A. corvina*) lies 32 miles northwest of Anguilla, bearing 311 degrees.

The largest specimen from Ile Frégate (KU 231097, 90 mm SVL) has a faint indication of paravertebral stripes anteriorly. It has spots, some of which join to form bars, on the sides extending only slightly onto the back. A smaller specimen (KU 231102, 77 mm SVL) has faint traces of all seven stripes at least anteriorly and some spotting on the sides. Other specimens are smaller and have distinct cream-to-buff stripes. There are no subcaudal stripes. These smaller specimens are brown above with a blue-green venter. This population is characterized by high incidence of anterior extension of the supraorbital semicircles. These extend to the middle of the second supraocular or farther. In all other populations of *A. plei plei* the majority of specimens have supraorbital semicircles which extend only to or not quite to the suture between the second and third supraoculars.

Large Ile Fourche specimens are uniform reddish-brown, with little or no dorsal pattern. There are spots on the sides, some of which form bars. A few specimens

have some spots extending onto the dorsum. There may be some black pigment in the scapular area. Small specimens have seven distinct stripes, and the light brown dorsal stripe may be broken into spots posteriorly. There are two black subcaudal stripes. In all specimens examined the preocular does not touch the supralabials. This is unlike most other populations of the subspecies (except Dog Island) wherein the majority of specimens have the preocular in contact with the supralabials.

Anguilla specimens are most similar in scale counts to specimens from St. Barthélemy, and differ significantly only in number of transverse rows of enlarged ventral scales (Table 1). In large specimens the cream-colored spots often join to form bars, especially on the flanks and on the posterior dorsum. The greenish-brown dorsum is darker than the sides. There may be some black suffusion in the shoulder area, but it never forms bars or bands. The hind legs are heavily spotted or barred. Striped specimens have two black subcaudal stripes.

Large specimens from Scrub Island are indistinguishable from those from St. Barthélemy and *Anguilla*. Striped specimens from Scrub Island are distinguished from those of other islands by the greater distinctness of the stripes. There are two black subcaudal stripes. Specimens from Upper Prickly Pear Cay differ the most in scale counts from other populations of *Ameiva plei plei* (Table 1). However, we regard differentiation of this population as insufficient to warrant recognition as a separate subspecies. The color pattern of Upper Prickly Pear Cay specimens is similar to that of other populations. The stripes, however, are vivid white and the background color is dark brown. There are two black subcaudal stripes. The spotted pattern is very similar to that of *Anguilla* specimens. Upper Prickly Pear Cay specimens do not attain the large size of *Anguilla*, St. Barthélemy, and Scrub Island specimens. The largest male collected was 116 mm SVL, and the largest female 78 mm SVL. No *Ameiva* were found on Lower Prickly Pear Cay on three collecting trips. Although the habitat is suitable and the island lies only 150 m west of Upper Prickly Pear Cay, no *Ameiva* occur there. In the absence of *Ameiva*, *Anolis gingivinus* was seen on the ground more often than in bushes, using the typical *Ameiva* habitat.

In the Dog Island population individuals do not attain large size as in some other island populations. The largest specimen collected was 119 mm SVL. Sexual size dimorphism is slight or nonexistent in this population. The largest male was 119 mm SVL and the largest female 85 mm SVL. There is greater sexual size dimorphism on other islands, with some populations showing large differences. On *Anguilla*, males reach 181 mm SVL, whereas females grow to 129 mm SVL.

The Dog Island population has a pattern similar to that of populations from other islands, but the spotted pattern is attained at a smaller size. The dorsal ground color is light brown. In some individuals between 73 mm and 80 mm SVL, the striped pattern is faded and some spots are present. The spotted or barred pattern is present at a minimum size of 83 mm SVL. In addition, specimens from Dog Island have a significantly lower number of dorsal granules at midbody, 145.0 ± 1.84 (135–159). In this character the Dog Island population differs from all other populations of *A. plei* and *A. corvina* but is not significantly different from *A. corax*. The Dog Island population is also characterized by the absence of prefrontal–supralabial contact, unlike all other populations of *A. plei plei* except that on Ile Fourche.

There are few specimens available from Ile Tintamarre (3), Ile Toc Vers (1), Ile Chevreau (4) and Scilly Cay (1). Each of these specimen's scale counts fall

within the range for *Ameiva plei plei*, and until additional specimens are collected these populations are assigned to *A. plei plei*.

Specimens examined.—St. Barthélemy: CM 118017–118025; USNM 236314; KU 231114, 231119, 231122, 231125–231130, 231136–231137, 231139–231143; MCZ 4357, 60593–60596, 77199–77203; additional specimens examined by DRP: LACM 62002–62005; KU 231115–231118, 231120–231121, 231123–231124, 231131–231135, 231138. Ile Frégate: KU 231097–231113; MCZ 77138–77142. Ile Fourche: KU 231086–231096, 79820–79823; MCZ 77143–77148. Anguilla: CM 114660–114680, 114684–114686, 114709–114716, 114722–114726, 114748–114756, 114773–114781, 115474, 115485, 115511–115517, 115522–115528, 115531, 115533–115534, 115544, 117900–117903, 117923–117925, 117934–117941, 117955–117964, 118026–118038; KU 231144–231146, 231161–231162; MCZ 6141; USNM 236281, 236283–236293; additional specimens examined by DRP: KU 231147–231160, 231163–231170; LACM 61995–62001; MCZ 77204–77210. Scrub Island: CM 115566–115567, 117965–117969; KU 79812–79814; ASFS x69, x85–87; MCZ 77131–77136, 77183; USNM 236298–236299; additional specimens examined by DRP: LACM 61991–61992, KU 231085; ASFS x70–84, x88–98. Upper Prickly Pear Cay: CM 114795–114797, 117983–117989. Dog Island: CM 114785–114793, 117949–117954; MCZ 77194–77195. Ile Tintamarre: MCZ 77196–77198. Ile Toc Vers: KU 231176. Ile Chevreau: KU 231172–231175. Scilly Cay: USNM 236296.

Ameiva plei analifera Cope, new combination

Ameiva analifera Cope, 1869:158 (part).

Ameiva pleii: Barbour and Noble, 1915:445 (part).

Lectotype.—ANSP 9080 (here designated), an adult, sex undetermined, from St. Martin, West Indies, collected by Dr. R. E. Van Rijgersma.

Paralectotypes.—ANSP 9073, ANSP 9077–9079, ANSP 9081, ANSP 9181–9182. Same locality as lectotype. Malnate (1971) also listed ANSP 9065, ANSP 9072, and ANSP 9074–9076 as syntypes of *Ameiva analifera*. ANSP 9065 is a specimen from St. Barthélemy collected by Dr. A. H. Goes and belongs to the subspecies *A. plei plei*. The other specimens (ANSP 9072, 9074–9076) do not belong to the species *Ameiva plei*. They are *Ameiva erythrocephala*. Cope (1869) did not mention these specimens in his description of *Ameiva analifera*; therefore, they should not be included in the series of syntypes of that species.

Diagnosis.—A moderate-sized subspecies of *Ameiva plei* (males to 139 mm SVL, females to 107 mm SVL) characterized by the combination of high number of granules at midbody, low number of femoral pores, moderate number of subdigital lamellae on the fourth toe, moderate number of scales in the fifteenth caudal verticil, and moderate number of enlarged transverse ventral scales (Table 2). The background color is gray-green with light spots (some forming bars) on the posterior third of the dorsum, and there are three to five vertical black bars or bands in the shoulder region (some not distinct). Juveniles are medium brown with very faint light dorsolateral stripes. Vertebral and paravertebral stripes are absent. The ventral scales are bluish-white to white with no pattern, and there are no subcaudal stripes.

Redescription of lectotype.—Cope (1869) did not designate a holotype when he described *Ameiva analifera*. However, he did give measurements for one specimen which he examined. These measurements are of ANSP 9080 and it is herein designated the lectotype of *Ameiva plei analifera*. It is an adult, sex undetermined, measuring 112 mm SVL, tail 216 mm (the distal 57 mm is regenerated). Dorsal granules at midbody 159; transverse rows of enlarged ventral scales 32; femoral pores 21 and 22 (total 43); 30 scales in the fifteenth caudal verticil; fourth toe subdigital lamellae 33 and 32 (total 65). The specimen is in poor condition, and its color is very faded. Spots, some of which join to form bars on the sides, are present. Posteriorly two rows of spots continue from the sides across the back. There are four transverse dark bars in the shoulder region which are broken middorsally. A fifth bar reaches to the middorsum on the right side. There is no ventral pattern. Cope described this subspecies as "Greenish yellow below, brownish olive above, . . ."

Distribution.—St. Martin/St. Maarten (Fig. 2).

Variation.—*Ameiva plei analifera* is a striped/spotted subspecies. The most obvious characteristics which differentiate *A. plei analifera* are the much faded stripes of small specimens, and the black shoulder bars of large specimens. None of the specimens examined have distinct stripes as in *A. p. plei*. Seven stripes are present in lizards ranging to 73 mm SVL, although the stripes are usually faded. Some small individuals may appear stripeless. The background color is medium brown to greenish-tan. Specimens between 73 and 83 mm SVL have no vertebral stripe and faded paravertebral, dorsolateral, and lateral stripes with spots on the flanks. Specimens larger than 84 mm SVL have white or greenish-white spots on the flanks and posterior back, some of which join to form bars. The hind legs and tail are spotted. The dorsal color is gray-brown. There are 3–5 black vertical bars or bands across the shoulder region; some may be faded. No other subspecies has black bars in this region.

Specimens examined.—ANSP 9073, 9077–9081, 9181–9182; CM 118039–118057; ASFS 19830–19840, 19842, 19844–19846, 19860–19877, 19941–19955; KU 231171, 231177–231184; MCZ 75078; additional specimens examined by DRP: LACM 62006–62007.

Ameiva corax, new species

Holotype.—MCZ 77137, adult male, from the south side of Little Scrub Island, off the northeastern tip of Anguilla, collected 23 May 1962 by Ronald F. Kliniowski (original number ASFS X100).

Paratypes.—(all from Little Scrub Island) CM 39503–39506; KU 79816–79819, 231185–231190; USNM 151832–151837; AMNH 92143–92146; UIMNH 55596–55599; UMMZ 125289–125292; LACM 61993–61994, 23 May 1962, Ronald F. Kliniowski. MCZ 77184–77193, 25 May 1963, James D. Lazell, Jr.; BMNH 99.5.29.12–99.5.29.18, J. W. Gregory; CM 115546–115564, 6 June 1987, E. J. Censky and D. A. Carty; CM 117970–117982, 8 April 1989, E. J. Censky and D. A. Carty; USNM 236300–236302, 8 October 1982, D. W. Steadman, G. K. Pregill, L. K. Gordon, and R. I. Crombie.

Etymology.—The name *corax* (Greek) meaning raven-black, refers to the coloration of the lizard, and alludes to its similarity to *A. corvina*.

Diagnosis.—A moderate-sized species (males to 132 mm SVL, females to 96 mm SVL) with low number of granules at midbody (127–159), high femoral pore count (58–72), moderate number of subdigital lamellae on the fourth toe (33–42), high number of scales in the fifteenth caudal verticil (28–38), and moderate number of transverse rows of enlarged ventral scales (30–37) (Table 2). The dorsum is black, sometimes dark brown, and patternless, and the ventral color is slate gray to black.

Distribution.—Little Scrub Island, off the northeast tip of Anguilla (Fig. 2).

Description of holotype.—Male, 111 mm SVL, head length 25 mm, tail length approximately 178 mm. Hemipenes everted. There are 142 dorsal granules at midbody; 36 transverse rows and 12 horizontal rows of enlarged ventral scales. Enlarged preanal scales arranged in a transverse row of four pairs decreasing in size laterally and three longitudinally oriented median scales, the central one largest and it and posteriormost one separating median pairs of transverse row. Femoral pores 32 on right leg, 33 on left leg. Fourth toe subdigital lamellae 38 on left leg. Tail scales in 34 rows at fifteenth verticil. Supraorbital semicircles reach to just anterior of suture between second and third supraoculars; the semicircle is composed of two to three rows of granules posteriorly. There are two subequal preoculars. The color is entirely black, with a blue-gray tinge below; the base of tail is grayish-white ventrally, tip brownish.

Variation.—This species is patternless and black. It differs significantly from *A. p. plei* and *A. p. analifera* in all characters. In addition, it differs significantly from *A. corvina* in fourth toe subdigital lamellae and femoral pore count. Another characteristic of this species is that the preocular is not in contact with the supralabials (see the account of *A. corvina* for further explanation).

There are two specimens which exhibit some remnant of pattern. MCZ 77193 is brownish-black with faded cream spots on the posterior dorsum and hind legs. There are two faint stripes on the neck. The belly is gray-black with cream-colored flecking in the midventral area and undersides of the legs, the subcaudals are light in color, and the chin is grayish-black. MCZ 76943 has a black dorsum with lighter stripes on the sides and hind legs.

Ameiva corvina Cope

Ameiva corvina Cope, 1862:312.

Lectotype.—ANSP 9116 (here designated), adult male, from Sombrero Island, collected by Mr. Hanson.

Paralectotypes.—ANSP 9115, 9117–9118 (two specimens are tagged 9117), 9120, 9122–9126, 9128–9130, 9134; MCZ 5532, 10535; USNM 52215–52216 (formerly MCZ 3616). Cope (1862) stated that the types of *Ameiva corvina* were in the Academy of Natural Sciences in Philadelphia (collected by Hanson) and the Smithsonian (collected by Riise). Barbour and Noble (1915) gave a partial history of the type specimens and concluded there were no specimens of *A. corvina* at the Smithsonian, but thought that any specimens originally at USNM had been given to the MCZ. Barbour and Loveridge (1929) listed MCZ 3613, 3616, 5531 (typographical error for 5532), and 10535 as syntypes. They stated that 3613 and 3616, formerly four in number, were part of the Riise Collection (USNM) accidentally returned by Cope with the Weinland Collection to ANSP. Two of the specimens were returned to the Smithsonian (USNM 52215–52216, formerly MCZ 3616, *vide* Cochran, 1961). In addition, there is no evidence in the MCZ catalog that 3613 was a specimen of *corvina*. Finally, Barbour and Noble (1915) listed ANSP 9115–9121 as “types” of *A. corvina*. However, Malnate (1971) listed the syntypes as ANSP 9115–9130. Actually, the type specimens at ANSP are 9115–9118 (two specimens are tagged 9117), 9120, 9122–9130, 9134, a larger series than reported by Barbour and Noble (1915) but with some specimens apparently now missing.

Diagnosis.—A species characterized by the combination of low number of granules at midbody, high femoral pore count, high number of subdigital lamellae on the fourth toe, high number of scales in the fifteenth caudal verticil, and high number of transverse rows of enlarged ventral scales (Table 2). Males reach a size of 133 mm SVL, females 87 mm SVL. This is a patternless species, dark brown to black above and slate gray to black below.

Distribution.—Sombrero Island, 32 miles NW Anguilla.

Redescription of lectotype.—Cope (1862) described the species and gave measurements of one specimen. As the measurements do not correspond to any of the type specimens listed, we assume it was one of the specimens now lost. We designate as lectotype ANSP 9116, adult male, with 105.5 mm SVL, tail length 210 mm. Dorsal granules at midbody 139; 34 scales in the fifteenth caudal verticil; femoral pores 35 and 32 (total 67); fourth toe subdigital lamellae 41; 34 transverse rows of enlarged ventral scales. The color of the specimen has apparently faded in preservative. It is now overall dull brown; there is no pattern.

Variation.—This species, like *Ameiva corax*, is patternless and black. It differs significantly from *corax* in the following characters: fourth toe subdigital lamellae 38.1 ± 2.2 (*corax* 36.8 ± 2.3) ($t_{(0.05)} = 2.048$, $df = 72$) and number of femoral pores 57.3 ± 3.22 (*corax* 62.1 ± 3.1) ($t_{(0.05)} = 5.412$, $df = 72$). It is significantly different from *A. plei* in all meristic characters.

One specimen (MCZ 6141) shows a trace of pattern. It has rows of faded spots on the posterior third of the dorsum and there are some black blotches on the sides of the neck. The venter is blue-gray.

Specimens examined.—ANSP 9115–9118 (two specimens have tags with ANSP 9117), 9120, 9122–9126, 9128–9130, 9134; MCZ 3616, 5532, 10535, 60621, 76940–76947; additional specimens examined by DRP: BMNH 67.11.4.1, 94.6.29.26; RMNH 3863, 28A–28F; UF 19417–19421.

TEMPORAL VARIATION

Examination of available collections of *Ameiva corvina* reveals temporal variation in meristic characters. Scale counts of specimens collected before 1900 are significantly different from counts of those collected since 1940 for all characters except fifteenth caudal verticil. In addition, specimens collected since 1940 are more similar to *A. corax*. When characters from all specimens (old and new) are analyzed together, the Sombrero Island and Little Scrub Island populations differ significantly in three of five characters: granules 139.1 ± 7.9 (*corax* 144 ± 7.2) ($t_{(0.05)} = 2.523$, $df = 80$); fourth toe subdigital lamellae 40.5 ± 2.8 (*corax* 36.8 ± 2.3) ($t_{(0.05)} = 4.469$, $df = 82$); transverse rows of enlarged ventral scales 35.3 ± 1.6 (*corax* 33.2 ± 1.6) ($t_{(0.05)} = 4.949$, $df = 84$). When the pre-1900 specimens are excluded from the analysis, the two island populations differ in only two characters: fourth toe subdigital lamellae and femoral pore count (see above). We have chosen to use only specimens collected since 1940 for comparisons because they more nearly represent the meristics of the present population. Though the current Sombrero Island population superficially resembles *Ameiva corax*, we recognize it as a separate species with similarities due to convergence.

Ford and Ford (1930) studied an isolated population of the butterfly *Melitaea aurinia* and found that, when the population was abruptly and drastically reduced in numbers, it became genetically more homogeneous. Subsequent increase in numbers increased variability. When the population stabilized, variability declined and homogeneity was reestablished. However, the new means for the population were different from those which existed in the previous stable period. It is possible that the temporal shift in scale counts of the population on Sombrero Island results from similar stabilizing selection following population size fluctuations.

Sombrero Island has been drastically altered since its discovery. In 1811, phosphate was abundant on the island. Between 1860 and 1880, much of the phosphate was quarried, reducing the island to a low, flat rock with many quarry holes (Bannis, 1978; Rigg, 1963). In addition, in 1898, a massive hurricane hit the island and "... swept over the island ... the keepers (of the lighthouse) thought the island was submerged" (log book for the Sombrero Light, kept on Anguilla). Less destructive hurricanes hit Sombrero in 1900 and 1928. The mining on the island and consequent destruction of habitat, coupled with the devastation of the hurricanes, undoubtedly had an effect on the size of the lizard population, possibly reducing it drastically. Since cessation of mining, lizard numbers have increased and stabilized, perhaps resulting in new meristic "norms."

The fact that the current population on Sombrero resembles the population on Little Scrub Island in both meristic data, color, and pattern can most easily be explained as convergence in similar habitats. Both islands are small (Sombrero Island is 3/4 mi long, 400 yd wide; Little Scrub Island is 1/4 mi long, 500 ft wide). Both islands are low, barren rocks without trees, and both support cactus, ground-trailing herbaceous plants, and small weeds (Lazell, 1964; personal observation). Thorpe and Brown (1989), in a study of microgeographic variation in lizard color patterns, found the cause of variation to be ecological conditions, rather than phylogenetic constraints.

MELANISTIC RACES OF *AMEIVA*

Melanistic races of lizards have been reported on many islands (Kramer, 1949; Mertens, 1934, 1952, 1963; Crisp et al., 1979). Several theories have been proposed to explain this phenomenon. Among them are Eisentraut's theory (as stated in Mertens, 1952) that the melanistic coloration is due to the nutrition derived from the type of plants on which the lizards feed. Another similar theory is that the increase in sea salts, due to salt spray, in the diet of lizards might be responsible for the dark coloration (Mertens, 1963; Carlquist, 1974). Kramer (1949) hypothesized that because these lizards live in a barren environment, exposed to intense radiation, the melanistic color provides protection from the damaging rays of the sun. However, two main theories have been advanced: the theory of thermoregulation and that of cryptic coloration. These theories need not be mutually exclusive.

Mertens (1963) was the first to advance the theory of thermoregulation as the cause for melanism in lizards that occur on islands in the Mediterranean. He refuted Eisentraut's theory of food type, stating that many melanistic forms feed solely on the abundant insect fauna. He also rejected the theory of cryptic coloration citing an island where dark lizards lived on light-colored rocks, though he did note that there were no apparent predators on the island (Mertens, 1952). He theorized that the proximate cause of melanism is thermoregulation. The dark coloration facilitates warming the lizard on cool mornings or in the cool season. He stated that black races do not occur on similar islands in areas where it is continuously hot, such as in the Red Sea.

However, three races of melanistic lizards have been found in the eastern Caribbean, a region where the climate is typified by constant mild temperatures. They are *Ameiva corvina* from Sombrero, *A. corax* from Little Scrub, and *A. atrata* from Redonda. It seems unlikely that in a constant mild environment a lizard would need an added catalyst to warm itself. Ernst (1982) questioned why more tropical versus temperate emydid turtles are black. He stated that the more rapid heating would be a disadvantage where the sun's rays are more direct and the temperatures are consistently high. He suggested that "good absorbers of radiant energy are also good radiators," and concluded that although the animals may heat at a higher rate, they also dissipate heat at a higher rate when they move into the shade. Norris (1967), however, stated that it has been wrongly assumed that because a reptile is visibly dark, it reradiates at a greater rate than light-colored reptiles. Visible color is not relevant to a lizard's capability to radiate. Both dark and light reptiles may emit long-wave infrared radiation, which is crucial to the energy balance of ectothermic animals, at the same rate per unit area. He further stated that the surface texture, rather than color, may be a better

indicator of a good reflector. Smooth or polished surfaces tend to reflect long-wave infrared radiation compared to rough or matte surfaces.

Crisp et al. (1979) found that experiments on the rates of warming and cooling indicate that the effect of color on heat balance is negligible for *Lacerta dugesi* of the Madeiran Archipelago under natural summer conditions. In addition to heat balance studies on variously colored free-ranging lizards, they used "model" lizards of matte black or reflective silver to assess the effects of surface color and shading on heat absorption. Their data showed that exposure to sun or shade makes a large difference in heat gain, but that the difference in color in constant sunshine affected heat balance only to a small extent. These results, coupled with the general resemblance between lizard color and color of substrate, led the authors to conclude that avoidance of predation is a better explanation than thermoregulation. Norris (1967) showed that background color-matching is a real phenomenon and that it apparently developed through predator pressure. In addition, Kaufman (1974) conducted predation experiments on light and dark-colored old-field mice (*Peromyscus polionotus*) and found that owls capture more of conspicuous than matching prey on both light and dark soils.

It appears highly unlikely that thermoregulation is the proximate causal factor for melanism in tropical lizards, especially for those living on dark substrate. Interestingly, the two black species in which dorsal granules were counted showed a reduction in the number of granules, and thereby an increase in the size of granules, in comparison with patterned species. It is possible that increase in scale size creates a more uniform surface which may actually reflect more long-wavelength infrared, thus inhibiting rapid increases in heat.

The most plausible theory to account for the melanistic races of *Ameiva* in the Caribbean is that of cryptic coloration due to selective predation. All three species occur on small (1 mi² or less) islands of dark substrate. There is little cover under which to hide. Seabirds, including frigatebirds, gulls, terns, tropicbirds, and boobies, are very abundant on these islands and are all potential predators. Gulls are known to be voracious and may eat almost anything. In addition to fish, they are known to feed on rabbits, squirrels, and rats (Terres, 1980). Frigatebirds regularly pick up young terns off the sand and snatch eggs from nests (Palmer, 1962). They also feed on sea turtles (Terres, 1980). Brown boobies have been seen feeding on *Ameiva* (R. Crombie, personal communication). As the diet of these birds appears to be relatively catholic, we cannot eliminate lizards, which often occur at high densities, as potential prey. To be camouflaged against the background would be highly advantageous to the lizard, especially in the presence of avian predators.

DISCUSSION

During the late Pleistocene (about 17,000 years ago), sea levels were much lower than they are at present. Emergent land masses in the Caribbean were larger and distances between them relatively shorter, especially in the northern Lesser Antilles. As sea levels rose, most of the land masses were submerged, leaving only isolated hills and ridges emergent. These are the present-day islands, each of which lies on a submerged bank, separated in many instances by great distances over water.

The most recent revision of *Ameiva* of the Lesser Antilles (Baskin and Williams, 1966) recognized 11 species, each occurring on a separate bank. When we compared the characteristics of species from banks south and east of the Anguilla

Table 6.—Summaries of data for *exsul*, *erythrocephala* and *griswoldi* (same data as for Table 1).

	Midbody granules	Ventral scales	4th toe lamellae
<i>erythrocephala</i>	204.3 ± 3.54 (187–214) N = 10	34.9 ± 0.18 (33–37) N = 10	40.1 ± 1.45 (33–37) N = 10
<i>exsul</i>	179.3 ± 4.30 (167–195) N = 10	36.1 ± 0.17 (33–38) N = 10	37.7 ± 0.71 (35–40) N = 9
<i>griswoldi</i>	159.0 ± 3.28 (145–174) N = 10	33.4 ± 0.14 (32–35) N = 10	34.1 ± 0.72 (31–37) N = 10
	15th caudal verticil	Femoral pores	
<i>erythrocephala</i>	38.9 ± 1.08 (33–41) N = 10	68.3 ± 1.25 (62–72) N = 10	
<i>exsul</i>	38.0 ± 0.44 (36–39) N = 10	33.4 ± 1.06 (31–39) N = 10	
<i>griswoldi</i>	29.7 ± 0.64 (28–33) N = 9	48.9 ± 1.74 (43–56) N = 10	

Bank, we found a strong meristic similarity between *A. plei* and *A. griswoldi* of the Antigua Bank (Table 6). *Ameiva erythrocephala* of St. Kitts Bank, although it occurs on a bank immediately south of the Anguilla Bank, shows very little meristic resemblance to *A. plei*. Previous workers have suggested a west-to-east direction of colonization rather than northward through the Lesser Antillean chain of islands (Gorman and Atkins, 1969; Williams, 1969). Biochemical and chromosomal studies on *Anolis* from the northern Lesser Antilles indicate that the invasion appears to have been from Puerto Rico eastward (Gorman and Atkins, 1969). In addition, *Sphaerodactylus macrolepis* from Anguilla appears to be of Greater Antillean affinity (King, 1962). However, when we compared *Ameiva exsul* (Table 6) from Puerto Rico with *A. plei*, the results do not change. We found stronger meristic similarity between *A. plei* and *A. griswoldi* than between *plei* and either *exsul* or *erythrocephala*. A discriminant function analysis scatterplot of all species placed *A. griswoldi* within the *A. plei* complex. *Ameiva exsul* and *A. erythrocephala* are distinct groups in this analysis.

Proximity of banks does not appear to be the only factor influencing dispersal. As the Antigua Bank is farther than the St. Kitts Bank from the Anguilla Bank, the similarity between *plei* and *griswoldi* appears paradoxical. However, when the banks were emergent, the distance between the Anguilla Bank and the Antigua Bank was considerably less than at present, and prevailing ocean currents in the region are in a general WNW direction. These two factors may have facilitated overwater dispersal between the two banks. A colonist leaving the Antigua Bank would be swept directly toward the Anguilla Bank, whereas one from the closer St. Kitts Bank would be swept westward, south of the Anguilla Bank. Although dispersal events may have been rare (Perfit and Williams, 1989), these data are highly suggestive of exchange of lizards between the Anguilla and Antigua banks, and not with the St. Kitts Bank, nor with islands farther to the west. We recognize that our data set for *exsul*, *erythrocephala* and *griswoldi* is small and that further investigation is needed. Although genetic similarity cannot be unequivocally inferred from meristic similarity, our data suggest affinity is not due solely to ecological constraints. The habitats of these islands are different from one another. An electrophoretic study, which is underway, may clarify this relationship.

As hypothesized, while the entire banks were emergent, exchange between the Antigua Bank and the Anguilla Bank could have been facilitated by the reduction in potential overwater dispersal distance. With submergence of the banks and resultant breakup of land into isolated islands, overwater distances increased and colonization events probably diminished, thus influencing divergence of populations. However, unlike some species of *Ameiva* (for instance *Ameiva auberi* in the Bahamas, Schwartz and McCoy, 1970) which have undergone rapid differentiation into a number of subspecies, *A. plei* remains relatively uniform throughout its range. This pattern of intraspecific variation is puzzling. Brown et al. (1991) examined intraspecific variation in *Chalcides* on Gran Canaria and Tenerife islands in the Canaries and found correlation primarily with ecological factors (humid vs. arid). Habitats on St. Martin and St. Barts (and their satellites) are grossly similar. Both are relatively mountainous with moderate rainfall. Anguilla and its satellites (and Tintamarre), in contrast, are flat, low, and dry. Yet *Ameiva plei plei* occurs on both Anguilla and St. Barts and all satellites, while *A. plei analifera* is found only on St. Martin. The black lizards of Little Scrub Island may be a case of rapid differentiation under extreme ecological conditions.

The addition of *Ameiva corax* to the Anguilla Bank fauna raises the number of

Ameiva species to two. Although this is the first report of two species on one bank in the Lesser Antilles, none of the other species complexes has been studied in detail.

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